CAUSES OF INJURY TO PLANTS RESULTING FROM FLOODING OF THE SOIL

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(WITH FIVE FIGURES)

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Introduction

This study was made in an effort to learn why saturating the soil with water causes almost immediate injury or death of many species of plants. While it has been shown that the deficient aeration accompanying flooding injures or kills the root systems, this fact does not explain why the shoots are injured so quickly. Injury is usually attributed to desiccation, caused by decreased water absorption through the injured roots; but this explanation seems inadequate. Plants can live for some days after the root systems are killed if the soil is kept saturated (**11**), and cut shoots can be preserved in good condition for many days in containers of water if the water is changed occasionally. Most species of plants can be grown fairly satisfactorily in shallow tanks of nutrient solution without forced aeration; but if the same species are grown in soil which is later flooded, the shoots are quickly injured. The injury of shoots cannot be caused entirely by injury to the roots as absorbing systems, because reduced absorption of water or of minerals cannot explain all of the symptoms observed in the shoots of flooded plants. Although wilting of leaves is often observed after flooding, this is not the only nor even the most characteristic symptom of injury.

Among the conspicuous symptoms of flooding injury is yellowing and death of the leaves, beginning with the lower ones and progressing up the stem. This chlorosis superficially somewhat resembles nitrogen deficiency, but often develops within four to six days after flooding, much too soon to be caused by nitrogen deficiency. The middle leaves of tomato show epinastic curvature within twenty-four to forty-eight hours after the soil is flooded; and lumps of callus tissue develop along the stem, particularly at the water level. In many species adventitious roots develop at the soil surface or just below the water surface where the water level is above the soil surface.

These occurrences cannot be explained fully as a simple result of desiccation caused by a damaged root system. Desiccation certainly would hinder the development of adventitious roots rather than stimulate their development. The epinastic curvature of leaf tips and the change in angle of petioles are also more characteristic of the reaction of turgid cells than of flaccid cells and wilted tissue. The rapid yellowing and death of the lower leaves might be caused by desiccation, or by toxic substances escaping from the dying roots or being produced in the soil which are carried upward in the transpiration stream. It, therefore, appears probable that the various symptoms produced by flooding have several causes and are not simply the result of interference with absorption following injury to the root system.

There is extensive literature dealing with the effects of aeration on root growth and absorption, but the causes of injury by flooding are not adequately explained. The reader is referred to the monograph by CLEMENTS (5) for the earlier work and to that of the writer (13) for more recent papers.

Effects of flooding on transpiration and water absorption

A number of measurements were made of the effect of flooding on water absorption and transpiration of potted plants, mostly of Marglobe toma-

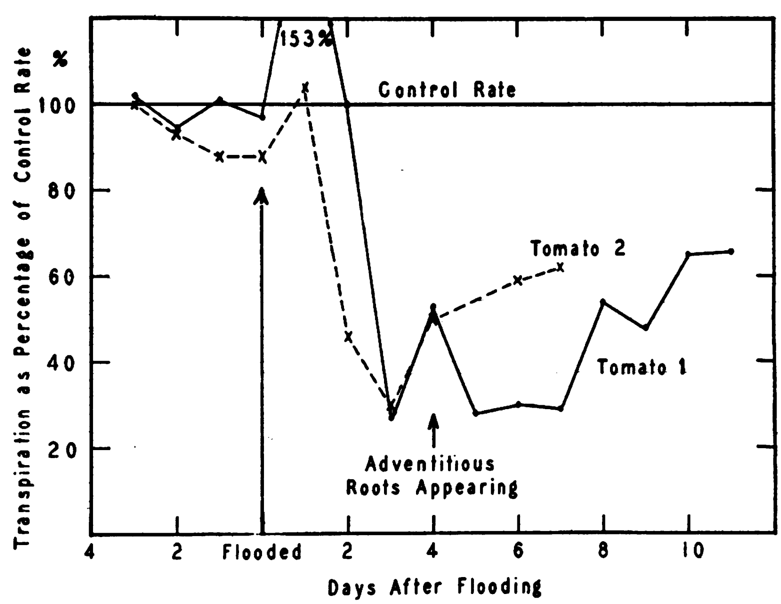

FIG. 1. Effect of flooding on transpiration of tomato plants. The values plotted are the averages of six plants. This experiment was performed in the greenhouse during the spring and summer.

toes. The plants were grown in four-inch pots of greenhouse soil until they were 15 to 18 inches high and had developed extensive root systems. For transpiration experiments, the pots were placed in metal containers and covered with oil cloth to prevent evaporation from the soil. The soil was maintained at approximately field capacity for the control plants and kept saturated by filling the containers with water for the flooded plants. Transpiration rates of two groups of tomatoes are shown in figure 1. The rate of the flooded plants is expressed as a percentage of that of the controls in order to minimize the effects of varying environmental factors on the shape of the curves. The two groups of tomatoes differed somewhat in behavior, the group flooded in the summer (group 1) showing a greater increase in transpiration immediately after flooding, a greater decrease after a few days, and a slower and less complete recovery than the group flooded in early spring (group 2).

Several measurements were made of the effects of flooding on the capacity of the roots to absorb and conduct water under a pressure gradient. Pots containing healthy plants were placed in an open tank of water. At intervals, several pots were removed to the laboratory, the shoots cut off, and the stumps attached to a vacuum pump by a system of rubber and glass tubing. The rate of water movement through these stumps under a pressure gradient of 20 cm. of mercury was observed for hour periods. The results of two experiments are shown graphically in figure 2. The pots containing the control root systems for this experiment were soaked in water for an hour in

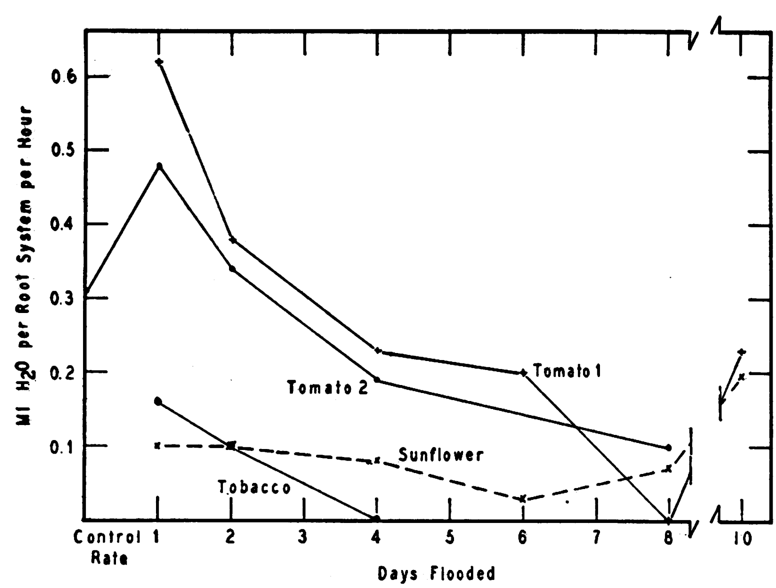

FIG. 2. Effect of flooding on water movement through detopped root systems under a pressure gradient of 20 cm. of mercury. The values for tomato 1 are the averages of eight plants, those for tomato 2, tobacco, and sunflower are the averages of three plants.

order to produce the same soil moisture conditions that existed in the flooded pots. In one experiment, sunflower, tobacco, and tomato plants were flooded and tested simultaneously to see if species differences were detectable. In all of these experiments, it was found that flooding for twenty-four hours stopped exudation from root systems not under pressure. Apparently even this short period of flooding was sufficient to produce serious injury to the roots. As shown in figure 2, large species differences were observed, tobacco roots being injured most and sunflower least severely.

In general, it appears that flooding causes a rapid decrease in the capacity of roots to absorb and conduct water, even from saturated soil. There appears to be some variation in the speed with which flooding acts, as indicated by the fact that one group of tomatoes showed an increase in water intake after 24 hours of flooding while another group showed a decrease after 24 hours. The writer found that exposure of root systems to a high concentration of carbon dioxide causes an immediate reduction in water absorption (**12**), and HOAGLAND and BROYER (**9**) later reported that exposure of tomato root systems to a high concentration of carbon dioxide causes an initial decrease in permeability, followed by an increase in permeability, which they attributed to injury of the roots. Perhaps the time required to produce the initial decrease in permeability followed by an increase varies with temperature, soil conditions, or other unidentified factors. Therefore, in some experiments the period of high permeability was observed; and in others it was already past before the first measurements were made. The increase in water absorption probably occurs because the cells are killed and resistance to water movement across the root cortex is decreased. It has been observed that when root systems are killed by heat or ether that permeability to water is greatly increased for a short time (**11**). Presumably the chief reason for decrease in water absorption during a prolonged period of flooding is plugging of the conducting system. This probably is caused partly by bacterial activity in the dying roots and partly by accumulation of gum or gum-like material in the region between dead and dying tissue. The writer (**11**) found that absorption of water through root systems killed by heat or ether was quickly reduced by gum accumulation in the region between the dead and living tissue at the base of the stem. The partial recovery which was observed in a number of these experiments after a period of several days was associated in all instances with the development of adventitious roots. Tobacco root systems showed no water absorption under pressure for a period of over two weeks, but after about three weeks some adventitious roots had developed, and considerable absorption occurred.

One experiment showing the effects of flooding on transpiration of woody species is included because it shows large differences in the reaction of two species. The results are shown in figure 3. Transpiration of privet decreased rapidly after flooding, and the plants were practically dead after 12 days, while transpiration of loblolly pine seedlings was still above the control rate and was not seriously decreased until after nearly a month of flooding. This is in accord with Hunt's report (**10**) that loblolly pine is very resistant to flooding. PARKER (**18**) has also published data showing large differences among woody species in respect to tolerance to flooding.

Observations on the effects of flooding

Several species of plants growing in pots of sandy loam soil were flooded and their behavior carefully observed. The changes in appearance of the shoots following flooding are believed to be as significant as the decrease in absorption and transpiration. The experiments with herbaceous species were performed in a sunny section of the greenhouse, most of those with woody seedlings out of doors. All of these observations were made during the summer. The pots were placed in metal tanks and tap water added until the level was one to two inches above the soil in the pots. In some experiments one set of pots was placed in a tank of water while another set of pots was buried in soil in a tank and then flooded.

Experiments with tomato

The first experiment consisted of three groups of Marglobe tomato plants about 15 inches high, growing in four-inch pots. Eight of these pots were kept in a tank of soil flooded to about 1.5 inches above the soil surface, eight pots were placed in a tank of water, and eight plants were kept watered to field capacity as controls. Symptoms of injury appeared within four days and were well developed in six days. The lower leaves were yel-

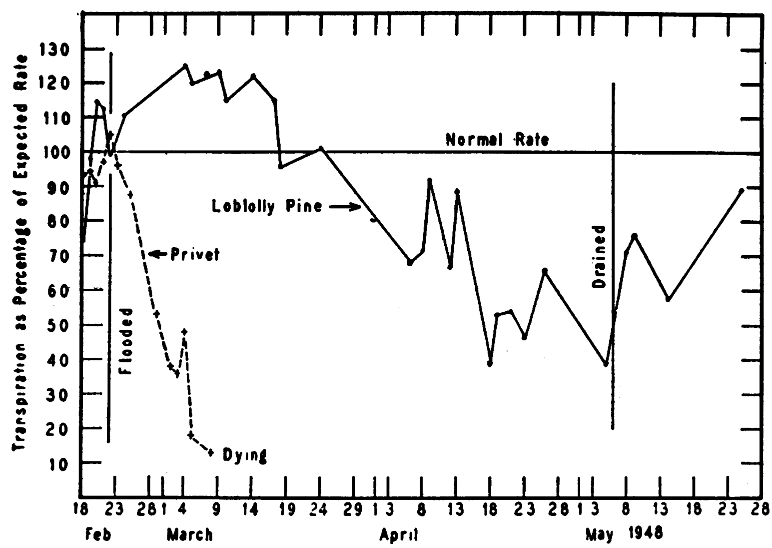

FIG. 3. Effect of flooding on transpiration of potted plants of privet (*Ligustrum japonicum* Thunb.) and loblolly pine (*Pinus taeda* L.). The values for privet are the average of three plants, those for loblolly pine the average of four plants.

low, and some were abscising; the middle and upper leaves showed definite epinastic curvature, the angle of the petioles with the stems being considerably greater than in unflooded controls. The bases of the petioles of tomato leaves usually form an angle of about 45 degrees with the stem, but those of flooded plants extended out horizontally or even drooped slightly. This is shown in figure 4. Lumps of callus tissue were visible about two thirds of the way up the stems of all the flooded plants, and considerable hypertrophy developed at the water line. The plants flooded in water were developing numerous adventitious roots, but relatively few had developed on the plants flooded in soil. After eight days of flooding, adventitious root development was much greater on plants flooded in water, and their tops showed distinctly less injury than those of plants flooded in soil. After twelve to fourteen days of flooding, the plants flooded in water had extensive adventitious root systems, the upper leaves were in good condition, and the plants were growing and flowering. Although some adventitious roots had developed on the plants flooded in soil, these plants were in distinctly poorer condition than the plants flooded in water. The shoots of the former were not growing appreciably; the latter seemed to be partially recovering. The water in the tank where the plants were flooded in soil had a somewhat lower oxygen content than the tank of water, possibly because the organisms in the soil surrounding the pots used considerable oxygen.

This experiment was repeated with a group of younger seedlings which were growing more vigorously. In addition to eight pots immersed in water and eight pots buried in flooded soil, eight pots were immersed in Hoagland's

FIG. 4. Appearance of flooded tomato plants. The plants in the tank on the left are unflooded controls, those in the center and on the right have been flooded for five days. Note the difference in position of the petioles of the middle leaves of the flooded and unflooded plants, also the dying lower leaves.

nutrient solution. This was done to guarantee an adequate supply of nutrients and compensate for whatever leaching occurred from the pots in tap water.

These plants were flooded in the afternoon, and the next morning some plants showed inrolling of leaf tips and drooping (not wilting) of the petioles of middle leaves. After two days of flooding (with cloudy weather and showers) many leaves showed distinct epinasty, and the bases of the petioles of most of the middle leaves were at approximately right angles to the stem instead of the usual 45-degree angle. Their appearance was somewhat similar to that of plants exposed to illuminating gas (see figure 4). After three days of flooding, the lower leaves of the plants flooded in soil were turning very yellow; those of plants flooded in water and nutrient solution were slightly less yellow. After four days the lower leaves of all flooded plants were dying, but injury was slightly greater on plants flooded in soil. Adventitious roots were developing on plants in water and nutrient solution, but not on those in the tank of soil. After a week the plants flooded in soil were definitely in worse condition than the plants flooded in water or in nutrient solution, all but the uppermost leaves being dead. Plants in nutrient solution developed slightly larger adventitious root systems than those in water, and plants flooded in soil produced relatively fewer and shorter adventitious roots. From the seventh to ninth days no further injury occurred, and the plants apparently were recovering somewhat. After nine days the pots were removed, drained, and left in the shade, where they began to recover slowly. All of the original root systems were found to have been killed, but the adventitious roots extended rapidly into the drained soil, especially on the plants flooded in water and Hoagland's solution. Apparently if the plants survive flooding long enough to develop a new adventitious root system, they will recover, though their growth has been severely checked during flooding. SARTORIS and BELCHER (**19**) mention that those varieties of sugar cane which produced few or no adventitious roots were most injured by flooding.

Simultaneously with these observations measurements were made of stem elongation and of transpiration. The results of the transpiration measurements are summarized in figure 1, group 1; the growth measurements are shown in figure 5. Growth almost ceased in a day or two after flooding but began to increase rapidly at the same time that adventitious roots began to develop. Perhaps this occurred because the new roots provided more water, but this group of plants never showed severe wilting. WENT (**22**) believes that the roots supply a hormone, caulocaline, necessary for stem growth and regards aeration as even more important for the production of this hormone than the salt absorption. If this is true, the resumption of shoot growth might be attributed to a renewed supply of hormone from the new adventitious roots.

EXPERIMENTS WITH SUNFLOWER

Pots containing sunflower plants about 50 inches in height were submerged in a tub of water. Another group of pots was buried in soil, and water was then added to a level about two inches above the level of the soil in the pots. The sunflower plants were injured relatively little as compared to tobacco and tomato. After a week one or two of the lower leaves were beginning to turn yellow, and the edges were drying out. The plants showed slight wilting the day after flooding, but did not show definite wilting again for a week, possibly because there was a little hot weather. After ten days, the plants showed relatively little injury, and the experiment was discontinued.

Adventitious roots appeared on all plants on the second or third day after flooding, and good adventitious root systems developed above the soil surface after a week. There was little, if any, difference between the adventitious root systems developed on plants flooded in water and plants flooded in soil.

Another group of six plants was flooded in water through which air was bubbled. These plants were no better in appearance and produced no more adventitious roots than the plants in unaerated water. Apparently sunflower plants are less easily injured by flooding than some other species. This agrees with observations on the effect of flooding on water intake and transpiration reported earlier in this paper.

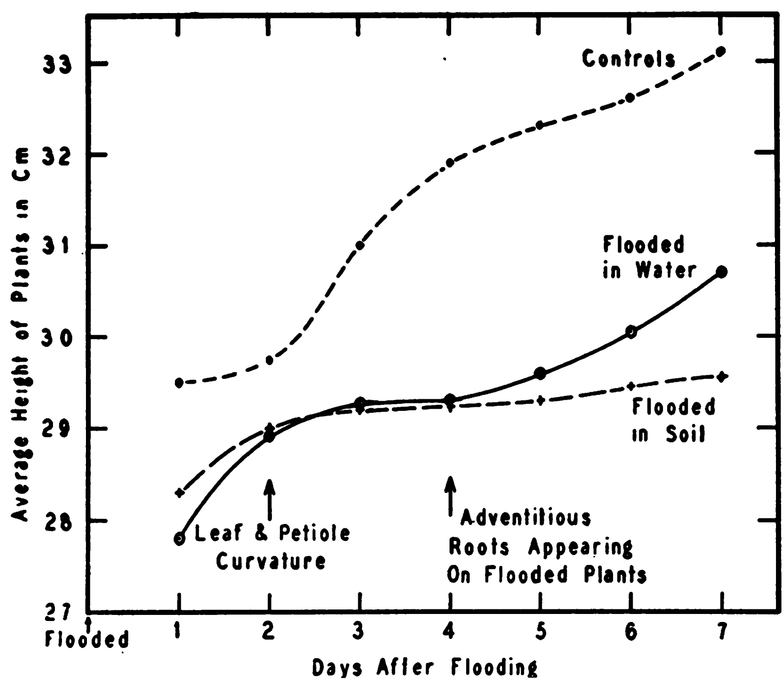

FIG. 5. Effect of flooding on stem elongation of tomato plants. Each value represents the average of eight plants.

EXPERIMENTS WITH TOBACCO

Previous experience indicated that tobacco is very sensitive to flooding, and this was found to be true in the present experiment. Plants 15 to 18 inches tall, growing in four-inch pots of greenhouse soil and in four-inch pots of sand, were flooded in tanks of water, sand, and soil. Half of these plants were potted in sand because previous experiments indicated more severe injury from flooding pots buried in soil. The weather was partly cloudy and showery during the first two days, clear and sunny the third and fourth days. In contrast to the sunflowers and tomatoes, which showed little wilting, tobacco plants were partly wilted on the second day and badly wilted after three days of flooding. In all three treatments the plants potted in soil were more seriously wilted after three days than the plants potted in sand. The lower leaves of all of the flooded plants were dead or dying. After a week the roots and most of the submerged portion of the stems of all flooded plants were dead. Very few plants produced adventitious roots. Although the lower and middle leaves were dead, the uppermost leaves were still alive and in good condition.

Experiments with yellow poplar

Previous experience with tree seedlings indicated that flooding the soil causes serious injury to some species. Parker (**18**) found, for example, that dogwood was severely injured or killed within a week, but red, white, and overcup oak survived for several weeks. Hunt (**10**) found that loblolly pine seedlings survived in saturated soil for ten months with no visible injury to the tops, though the roots were severely injured. Yellow poplar seedlings in their third growing season were used in these experiments. The pots containing one group of seedlings were flooded in water; the pots containing another group of six seedlings were buried in soil and flooded. These plants were left out of doors. After five days one tree flooded in soil was dead, and the lower leaves of the others were dying, although none of the youngest leaves were wilted. The leaves turned yellow and then brown, and some were strongly mottled. The petioles tended to droop until they were at right angles to the stem, as with tomato. Similar symptoms existed on the trees flooded in water but to a lesser degree, and none of them were dead. After seven days all leaves on the plants flooded in soil were dead, but only half of the trees flooded in water were dead. After 12 days all the leaves of all but one tree in water were dead, and it bore only one or two living leaves.

A second set of five yellow poplar seedlings was flooded in water for two weeks. After this interval four trees were completely dead, but the upper four or five leaves of one tree were still healthy, though the lower ones were yellow and dying. The submerged portion of the stem of this tree was covered with small, white protuberances which resembled adventitious roots. This plant was transferred to a bucket of water and kept alive for about six weeks. In other experiments the lower part of the stems of several yellow poplar seedlings were enclosed in glass tubes, which were kept full of water. Considerable enlargement of the more deeply submerged portions of these stems occurred, producing an effect similar to the buttressed bases often found on cypress and tupelo gum trees growing in swamps.

Discussion

Considerable differences existed in the response of the various species to flooding. Tobacco wilted severely almost immediately, but sunflower wilted only slightly and showed little evidence of injury, while tomato wilted little or moderately, yet it showed severe injury. These results suggest that desiccation is not the only important cause of injury. The degree of injury was least in sunflower, which was the first species to develop adventitious roots, and greatest in tobacco, which was slowest to develop adventitious roots; but it is difficult to decide which is cause and which is effect.

The data shown in figure 2 indicate that the absorption of water was reduced most rapidly and to the greatest extent in tobacco and to a lesser extent in sunflower, with reduction of tomato intermediate. It seems possible that the rapid development of adventitious roots on sunflower largely compensated for the loss of the original root system, but in tobacco the original roots all died before enough adventitious roots developed to effectively replace them.

In all experiments plants in pots buried in flooded soil suffered more injury than plants in pots standing in water. Surrounding the pots with soil prevented convection currents which might have carried some oxygen to the bottom of the tanks. Furthermore, the soil undoubtedly contained numerous microörganisms which must have used considerable oxygen. That the soil organisms play a part in causing injury is further suggested by the fact that tobacco plants potted in sand, which probably contained relatively fewer organisms than the soil, showed less injury under all conditions of flooding than plants potted in soil. Nevertheless, all plants showed injury when flooded. On the other hand, when bases of cut shoots are immersed in water, little or no injury occurs to the leaves; and adventitious roots are soon developed. This suggests that the dying root systems themselves are in some manner directly or indirectly related to the injury to the shoots.

The large reduction in water absorbing capacity of the root systems which follows flooding might seem adequate to explain the injury to the shoots. While lack of water may be an important factor in the death of the leaves, it cannot explain the curvature of the leaf tips, the change in angle of the petioles, the hypertrophy of stems at the water line, nor the development of adventitious roots. All of these occurrences are more likely to take place in turgid, growing tissue than in flaccid, wilted tissue; and they are more likely to be related to disturbance of translocation of carbohydrates and possibly of hormones than to dehydration.

Conditions are unfavorable for the translocation of organic compounds into the roots, or even below the water line. Not only is the consumption of carbohydrates in the roots greatly reduced or even ended within a few days, but the oxygen deficiency below the water line doubtless inhibits the translocation process itself. CURTIS (**6**) and MASON and PHILLIS (**15**) found that exclusion of oxygen from a portion of the stem greatly reduces the transport of carbohydrates, and DUBUY and OLSON (**7**) reported that movement of auxin in Avena coleoptiles is prevented by lack of oxygen. Interference with downward translocation probably results in accumulation of carbohydrates in the lower part of the stem, near the water line, causing hypertrophy and the development of adventitious roots. Accumulation of auxin in this region might accentuate the effects of carbohydrate accumulation on hypertrophy and root initiation. The epinastic curvature of the leaves and change in angle of the petioles of the middle leaves might also be caused by an excess of auxin in the lower half of the stem. This change in angle was most pronounced in tomato but also occurred in yellow poplar. CHILDERS and WHITE (**4**) noted that the younger leaves of apple trees assumed a somewhat wider angle with the stem after the root systems were flooded, but did not discuss the cause of the phenomenon. The lower leaves of the plants in our experiments were probably too old or too quickly injured to show much response, and perhaps not enough auxin accumulated in the upper part of the stem to affect the upper leaves. There is no direct evidence to support this hypothesis, but it is an attractively simple method of explaining most of the phenomena observed to occur in stems of flooded plants. It might possibly be extended to explain the development of buttressed bases of cypress and tupelo gum trees growing in partially flooded areas. The author intends to test this hypothesis in the near future.

The yellowing and death of the lower leaves may in some instances be caused by desiccation, but it seems more likely that it is at least partly the result of poisoning by toxic substances moving up from the dying roots. These substances might be escaping from dying cells, or they might be products produced by microörganisms on the roots or in the soil. Since cut shoots of tomato can be rooted in water with little injury to the leaves, although injury occurs when the roots are left attached, it appears that the roots contribute to the injury of the shoot in some manner. Plants in pots buried in soil and flooded showed more injury than plants in pots submerged in water, and plants growing in pots of sand were injured less by flooding than those growing in pots of soil. This probably was related to decreased oxygen supply, resulting both from physical interference with oxygen movement by soil and from increased oxygen consumption by microörganisms in soil as compared to sand. Under anaerobic conditions there is much greater likelihood of the production of reduced compounds such as nitrites and sulphides which are toxic to roots and, if carried upward in sufficient quantities, might poison the leaves. It may prove difficult to ascertain the nature and role of such substances, but the problem is worthy of investigation.

Flooding probably almost completely stops the absorption of nutrients from the soil until the roots are killed. After the roots begin to die, whatever solutes are present in the soil solution are probably absorbed with the water, since the dead root cells are no longer differentially permeable. It therefore seems unlikely that deficiency of nitrogen or mineral nutrients is an important factor in injury to the shoots of flooded plants. It must be admitted, however, that the appearance of plants in flooded soil often suggests that they are suffering from mineral deficiency.

One other problem deserves mention. Although all of the roots originally present on flooded plants are usually killed, the new adventitious roots often grow vigorously. Furthermore, most of the species which are injured by flooding can be grown successfully in water culture. BERGMAN (**1**) found that if the water in which the pots containing Pelargonium, Impatiens, and Phaseolus were submerged was aerated, after a week or ten days adventitious roots developed and the plants could then grow without aeration. This is another example of the difference between roots developed in soil and in water. This suggests that the roots which are produced in water are different anatomically or physiologically, or both, from roots produced in well aerated soil. It has been observed that roots produced in poorly aerated media usually contain much larger intercellular spaces than roots produced in well aerated media. BRYANT (**2**) reported that barley roots grown in unaerated cultures had more air spaces in the cortex, thinner cell walls, and a tendency to be differentiated closer to the root tips than roots in aerated cultures. SCHRAMM (**20**) found that roots of barley, corn, oats, and tomato grown in unaerated culture solutions all contained numerous large air spaces in the cortex and were less suberized than roots produced in aerated cultures. MCPHERSON (**16**) observed that more extensive development of air spaces in corn roots occurs in wet soil than in dry soil and in unaerated than in aerated culture solutions. Aeration with 50% oxygen and 50% nitrogen resulted in almost complete elimination of air spaces and excellent root growth. McPherson concluded that the air spaces were produced by collapse of cells following their death from lack of oxygen. Barley and oats were reported to behave in a similar manner, except that their oxygen requirement was lower than for corn roots.

It has generally been assumed that the air spaces result in a more adequate supply of oxygen to the cells of the roots, but the writer knows of no direct proof of this. CANNON (**3**) has presented evidence that oxygen produced by photosynthesis diffuses down to the roots of willow, and GLASSTONE (**8**) has shown that gas moves freely through the stems and roots of many plants under a slight pressure gradient. Nevertheless, it has never been demonstrated that the cells of roots with a cortex containing large air spaces are any more adequately supplied with oxygen than those in roots containing a very compact cortex. According to MCPHERSON (**16**) development of air spaces is caused by lack of oxygen, and by the time the air spaces have developed the period of most rapid metabolic activity and highest oxygen consumption probably has passed. It would seem, then, that by the time the air spaces have developed the greatest need for aeration has already passed.

It is quite possible that an important reason for survival of roots developed under water is that they are physiologically different from those produced in well aerated media. Perhaps because of differences in their respiratory enzyme systems they can actually function with a lower supply of oxygen. It would be no more difficult for a poorly aerated environment to produce differences in the physiological characteristics of roots than for it to produce the differences in structure which have been observed. Roots are physiologically different from shoots in several ways (**13**, p. 161).

Changes in enzyme systems sometimes occur during plant development. MARSH and GODDARD (**14**) and MERRY and GODDARD (**17**) found that cytochrome oxidase, which is an important enzyme in young leaves, is absent or at least not essential in the respiration of mature leaves of carrot and barley. The possibility of changes in oxygen requirement of tissue is supported by the observation of STEWARD, BERRY, and BROYER (**21**) that cells developed in water will absorb salt and respire normally at a lower oxygen concentration than cells developed in a well aerated medium.

Summary

A series of experiments was performed to learn how flooding the soil in which plants are growing causes injury or death of the shoots. Flooding is followed by a rapid reduction in transpiration and the water absorbing capacity of the roots and usually is followed by more or less wilting of the shoots. Within three or four days the lowest leaves begin to turn yellow and die, the middle leaves of tomato and yellow poplar show epinasty, and adventitious roots begin to develop on some species.

Injury to the shoots was found to be more severe when the pots were surrounded by soil and flooded than when they were simply submerged in water. Plants potted in soil were injured more than plants potted in sand. Tobacco was most injured by flooding, sunflower least, and tomato was intermediate in degree of injury. Those plants which produced adventitious roots most rapidly suffered least injury and showed the greatest degree of recovery.

While lack of water might explain the death of the leaves, it cannot explain such characteristic effects of flooding as curvature of the leaf petioles, hypertrophy of stems at the water line, nor development of adventitious roots. Flooding probably stops downward translocation of carbohydrates and auxin, and possibly their accumulation at the water line is responsible for hypertrophy and development of adventitious roots. Accumulation of auxin in the lower half of the stem might also be responsible for the epinastic curvature of the leaves and petioles. The injury and death of the leaves may be caused at least in part by toxic substances moving up from the dead roots or even from the surrounding soil.

It is believed that injury to the shoots of flooded plants is complex in origin and has several causes rather than resulting simply from interference with water absorption.

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